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OBSERVATIONS ON THE NATURAL HISTORY OF THE WESTERN BANDED GLOWWORM ZARHIPIS INTEGRIPENNIS (LE CONTE) (COLEOPTERA: PHENGODIDAE)

By

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ABSTRACT: The life history of the phengodid beetle Zarhipis integripennis (Le Conte) is covered in most of its stages. Included are observations on other species of Zarhipis and the Brazilian "Railroad Worm," *Phrixothrix*, as well as notes on the millipeds upon which these insects feed.

INTRODUCTION

Since 1887, very little information has been published on the natural history of phengodid larvae—glowworms with luminous bands on the dorsal surface of each abdominal and thoracic segment. The literature on *Zarhipis* larvae in particular has been minimal. Most of the available material is in the form of notes published from presentations to various entomological society meetings.

Rivers (1886a), undoubtedly referring to Zarhipis, was the first to note that the insect feeds on millipeds. He reported that the larvae feed on both Polydesmus and Julus and suggested that they prefer Julus because of its larger size. Later, he described the adult female and referred to the pupa (Rivers, 1886b). He also mentioned the close relationship in the life history of *Phengodes* and Zarhipis (Rivers, 1887), but did not go into detail. Charles V. Riley (1887) published some notes on the larva and larviform female of Zarhipis and Phengodes. The late Herbert S. Barber, who worked out much of the biology of the related forms of *Phengodes* of the eastern United States, published most of his findings as notes also.

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DEC 6 1967 WOODS HOLE, MASS The purpose of this paper is to present the results of a six-year study made on the natural history of Zarhipis larvae. Three species of this insect are known (Linsdale, 1964)—Zarhipis integripennis, Zarhipis truncaticeps, and Zarhipis tiemanni. This paper is primarily concerned with Z. integripennis (Le Conte), which is distributed throughout California. Records indicate that this species has also been found in Washington, Oregon, and Baja California. To distinguish Z. integripennis from the luminous lampryid larvae in which the luminous areas are restricted to the posterior abdominal segments, the common name "Western Banded Glowworm," is being applied.

Included in this presentation is a description of the eggs, the larvae, the female and male pupae, and the adult female. Observations made on the mating and feeding behavior of this species are reported, and methods of collecting, rearing, and preserving larvae are discussed.

ACKNOWLEDGMENTS

This paper would not have been possible had it not been for the close cooperation of Dr. Donald D. Linsdale in the exchange of scientific information. He very graciously made his valuable library of notes available to the author. This collection contains almost every piece of information that has been published on the family Phengodidae. Through the efforts of Dr. Linsdale, the author had the opportunity to read the unpublished notes of Drs. J. W. MacSwain and F. X. Williams, both of whom in recent years have made observations in depth on Z. integripennis in environments other than the desert areas.

Dr. Elbert Sleeper, California State College, Long Beach, made available 13 Zarhipis larvae collected in Joshua Tree National Monument, California. All of the millipeds observed in this study were determined by Dr. Nell B. Causey, Louisiana State University. Her immediate responses to inquiries and her help-ful cooperation were stimulating. Mr. L. W. Nichols deserves mention for his encouragement ("go ahead—take another shovelful") and help during the six years this work was in progress. Members of the author's family contributed much to the success of this labor in giving up many week ends to help collect Zarhipis larvae.

LIFE CYCLE

EGGS. In some unpublished notes, Williams described some Z. integripennis eggs as being round, measuring approximately 2.75 mm. in diameter; and some as being oval, measuring up to 2.75×2.40 mm. Linsdale (1961) reported eggs measuring from 3.0 to 3.3 mm. in length. This variation in egg size may reflect a difference in the size of the females.

DESCRIPTION. When freshly laid, eggs of Z. *integripennis* are pearly white, elastic to the touch of a teasing needle, and show no micropyle. They are

transversely round and longitudinally elliptical. This shape becomes more evident as the larvae mature in the eggs. As the eggs mature, they collect enough fine dust to give them a light gray appearance. Mature eggs have a double chorion; the thinner, more transparent inner layer may be exposed by using a needle to flake off the outer chorion.

OBSERVATIONS. The first eggs observed in this study were laid on 1 May 1962 by a female collected from Short Canyon, Kern County, California. She produced a total of 23 eggs by 7 May. (This should not be assumed to be an average egg production since, in 1961, Linsdale reported 92 eggs from one female.) The first weak glow from the eggs, noticed on 2 June, was not as bright as that of the female, which was still alive. The female died about the same time as the larvae in the eggs became visible—about 20 June. The larvae were curled in an almost complete circle with their glowing bands brightly visible. A color photograph taken with a time exposure of 1 hour clearly shows the luminous bands of the developing larvae. The chorion itself does not glow.

The eggs from the Short Canyon female were kept in a garage with unregulated temperatures at the U. S. Naval Ordnance Test Station (NOTS), China Lake, California. In this environment, it took the eggs 33 days to become luminous and 63 days to hatch—the first larva hatched 2 July, the last emerged 9 July. This experiment compared favorably with the 1961 study made by Linsdale, who reported that eggs kept at regulated moderate temperatures in a Berkeley, California, laboratory took 32 days to become luminous and 50 days to hatch.

On 4 March 1962, a large $(65 \times 8 \text{ mm.})$ Z. integripennis female larva, collected in Berkeley by Linsdale was received for study. This specimen matured on 28 April, was mated on 2 May with a male Z. integripennis that had been collected from Short Canyon, and produced its first eggs on 2 June. These eggs were about one-half the size of eggs produced from a normal mating with a male and female from the same population. About 20 small eggs were laid when production suddenly changed to eggs of a normal size. However, none of the eggs matured, suggesting that the female could be from a sibling species. Further experiments should be undertaken to determine the validity of this study and to determine the degree to which speciation may have proceeded.

LARVAE. Zarhipis larvae have been described in varying detail by several authors. Rivers (1886b) described the larviform female and commented on its similarity to the larva. Riley (1886a, 1886b, 1886c) compared them with *Phengodes* larvae and Williams included a sketch of the head of a *Zarhipis larva* in his unpublished notes. Peterson (1957) gave a generalized description of the larvae of the family of Phengodidae and Linsdale (1961) described the larva in his doctoral thesis.

DESCRIPTION. First instar larvae resemble mature larvae in structure but



FIGURE 1. Zarhipis integripennis biting a milliped in the most vulnerable place, the articulating membrane between the head and the first body segment.

not in coloration. They are white and somewhat translucent with black eyes, brown mandibles, and dark brown tarsal claws. Newly hatched larvae are relatively large for insects. Eight from one female varied in length from 11 to 19 mm. The larvae are ambulatory as soon as they are hatched and have been observed to explore their container, burrowing under the sand at times. They glow brightly in bands in the same manner as mature larvae. After feeding they become turgid and material may be seen in their intestines.

Second instar larvae deserve special mention in that, under natural desert conditions and probably in general, they are the first feeding stage.

The number of instars of Z. *integripennis* is not known. Measurements of the head on cast larval skins indicate that Zarhipis do not obey Dyar's law. One larva, collected on 23 May 1959, lived until 28 August 1960. It cast its skin six

Plate 1

UPPER FIGURE. Two Zarhipis integripennis males fighting. Males will not ordinarily fight each other unless in the presence of a female.

LOWER FIGURE. Zarhipis integripennis larva feeding on the terminal segments of Atopetholus michelbacheri. Note the translucent walls of the diplosegments, indicating digestion is starting in the milliped as the larva feeds.

PROC. CALIF. ACAD. SCI. 4TH SER., VOL. XXXV, NO. 12 (TIEMANN) PLATE 1





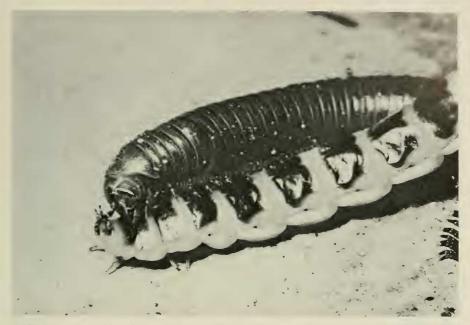


FIGURE 2. Zarhipis integripennis larva towing a milliped. Towing is usually accomplished by pulling on an antenna, however, a leg is sometimes used.

times—19 July, about 11 September, 12 October, 25 November, 11 January, and 22 February—without marked increase in size. On 26 May, this specimen measured 43.5 mm., 10 months and seven instars later, it measured 50×7 mm. These measurements were taken of the walking larva and are probably accurate to within 3 mm. in length and 1 mm. in width.

Aestivating larvae cast their skin once in the late spring to spend the summer in a cell in a light color stage. Although physically the same as active larvae during this period, pigmentation of the exoskeleton is reduced to very light triangular patches on the dorsum. In the fall (while still in the cell and without having eaten) they again cast their skin, returning to their usual dark pigmented stage. If an aestivating larva is activated by the addition of moisture and a reduction in temperature, it will feed as usual on millipeds.

The winter phase of the female Z. integripennis larvae described here is based upon the writer's notes and refers to previous descriptions only when the material has been personally authenticated. The male larvae, in most aspects including luminosity, are very much like the female. Therefore, they are described only when some contrast with the female is apparent.

In general appearance, larvae are elongated and orthosomatic. The mature female larvae range in size from 40 to 65 mm. Because of their vigorous activity,



FIGURE 3. Zarhipis integripennis larva starting to remove the head of a milliped prior to feeding.

only one of the three male larvae collected for this study was measured. This male measured 32×3 mm, during the last larval instar.

Coloration of the larvae varies somewhat from specimen to specimen and from male to female. On specimens collected from the mountain and coastal regions, the first two tergal segments are usually black and the colored portions of the terga are outlined with a border of color ranging from cream to yellow. The desert specimens generally have a reddish colored dorsum on the first two segments of the thorax. In color, the third segment of the thorax and the entire abdominal terga range from black to tan. The entire dorsal surface is shagreened and, except for the spiracles, the ventral and lateral surfaces range from cream to yellow. The intense dark pigmentation of the female was not present on the male larvae observed in this study. Instead, they had light tan triangular patches of color on each tergum.

The head is prognathous, retractable, and without epicranial suture. It is about one-half the width of the prothorax. Antennae are three-segmented. The second segment has a ventral sensory disk at the apex. The smaller third segment usually has one or more setae at the apex with two long setae at the

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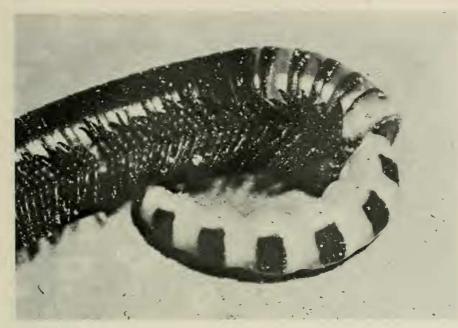


FIGURE 4. Usual feeding posture of Z. integripennis.

base. The eyes consist of an ocellus located on the side of the head posterior to, and almost touching the base of the antennae.

The labrum is fused to the clypeus and frons. The mandibles are similar in shape to a thin sickle (sharp, pointed, and curved). They have a channel covered with a strong, close-fitting seta that makes a hollow passage. The mandibles overlap by about one-third their length and are crossed over the hypopharnyx. Three long setae are located on each side of the nasal. Two short curved setae, pointed anterior to the nasal front, almost meet over the hypopharnyx.

The three segments of the thorax, nearly equal in length, widen progressively until the apex of the prothorax is approximately one-third the width of the base of the metathorax. The terga of the pro- and mesothorax are finely punctated, with each puncture containing a small seta. These setae are closely appressed in live specimens and point to the posterior. Three long setae are located on the terga of each side of the prothorax, just outside of the pigmented areas. A single bilabiate spiracle is located on the parascutal area of the mesothorax with a pigmented area anterior to the spiracle.

The legs are four-segmented with sharp pointed tarsungulus. The segments consist of a coxa, a trochanter, a femur, and a tibia. A line of strong hair-like setae, pointed forward laterally, extend along a ridge on the coxae. The distal half of the trochanter has hair-like setae which are pointed downward and in-

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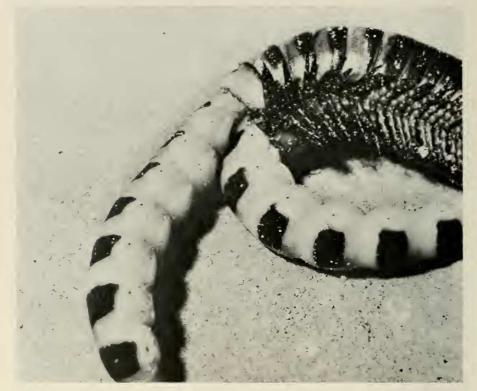


FIGURE 5. Two Z. integriptennis larvae feeding on a milliped at the same time. This was observed in nature, and was a frequent occurrence in captivity.

ward. The femur has two types of setae; one type, arranged in a comb-like manner in three ill-defined rows on the inner side, is short and heavy, the other type, located on the under surface of the segment, is longer and hair-like. Both types point downward. The tibia has hair-like setae which are pointed downward and one short and heavy seta situated adjacent to the tarsungulus.

The ten-segmented abdomen widens progressively from the first to the fourth or fifth segment; from this point it gradually narrows to the ninth segment. The tergum of the ninth segment covers the pleural area. From one to three closely

PLATE 2

UPPER FIGURE. A male pupa of Zarhipis integripennis showing the luminous areas. Photograph was made by double exposure.

LOWER FIGURE. A female pupa of Zarhipis integripennis showing the luminous areas. Photograph was made by double exposure. PROC. CALIF. ACAD. SCI. 4TH SER., VOL. XXXV, NO. 12 (TIEMANN) PLATE 2







FIGURE 6. Zarhipis integripennis larvae feed under the ground surface. After light rains have caved in the ground surface, pits containing milliped diplosegments may be found.

set setae may be found on each side of the ninth abdominal tergum. The small tenth segment is used as a proleg in locomotion, and in an opposable manner when capturing prey. Setae ring the anus. The spiracles, located on the parascutal area of the first to the eighth segments, are bilabiate and have a pigmented triangular patch anterior to the opening. A single seta is located on each abdominal pleura. Female larvae have a circular concavity which male larvae lack, with a long setae on each side of the sternum of abdominal segments one through eight. Segments one through nine have from one to three setae on either side of the posterior half of the sternum.

There are two U-shaped spiracle-like pores situated on either side of the medial line and located about one-half the distance to the edge of the dorsum of abdominal segments two through nine. These pores are hidden beneath the fold of the preceding segment, becoming visible only when the larvae are feeding and when they are turgid. If a larva is handled roughly, a drop of clear amber material is excreted at one or more of these pores (rarely from more than two pores at a time). This material is water soluble, odorless, slightly viscous, and dries rapidly to an amber solid. The purpose of the excretion is not evident.

Zarhipis integripennis larvae apparently have no voluntary or immediate control over their luminescence. One exception was noted by both the author

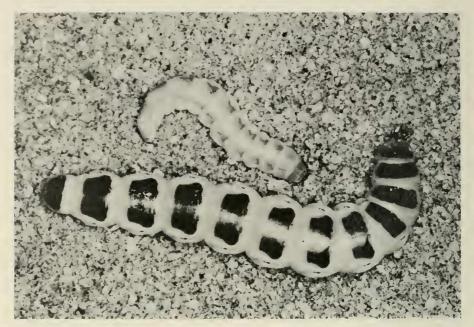


FIGURE 7. Last larval instars of a male and female of Z. integripennis.

and Linsdale—the luminescence in one larvae increased brightly when photographed by electronic flash. Subsequent photographs made with electronic flash were taken of many specimens with no noticeable change in their luminous intensity.

OBSERVATIONS. One male larva, collected at the mouth of Short Canyon on 11 January 1962 during shallow digging (probably no deeper than 15 cm.), was at first thought to be injured. However, it pupated 16 days later indicating that the larva was in a precast period and that in all probability this is the depth at which the male pupa may be found.

On the night of 24 February 1963, four *Zarhipis* larvae were collected. One was active under a board and three were collected in traps made of one-gallon cans. The larvae were examined for luminescence in the field before they were disturbed. One, dying from exposure in the trap, was glowing feebly. No luminescence was visible on the other three specimens, although the night was dark and moonless. When the specimens were examined about 45 minutes later, they were all glowing brightly. The apparent conclusion is that active hunting larvae do not glow.

In April, 1963, a female Z. *integripennis* was mated and left in a large (50 cm.) wastebasket filled with sand and fitted with a screened drain. Eight fairly mature larvae were also placed in the wastebasket. The primary objective



FIGURE 8. A female and male pupa of Z. integripennis.

of this study was to find out how deep the female would burrow. Water was not added to the wastebasket after 22 April and the sand was allowed to become dry.

When the weather became cooler, around 11 October, the sand was moistened with an inch of water with an additional inch added on 13 October. A 16×1.5 mm. *Zarhipis* larva was found on the surface on 16 October and by 18 October, 21 larvae had surfaced. These larvae ranged in size from 14×1.5 mm. to 17×2 mm. They were miniature replicas of the mature female both in pigmentation and in the round concavities on the sterna. While examining the larvae, it was noted that they would climb a teasing needle (held at an approximate 45° angle) in the same manner they would ordinarily use to capture a milliped.

On 23 October the sand was carefully removed from the wastebasket. The dead body of the female was found at a depth of 18 cm. and 19 cast skins of first instar larvae were found clustered close to her body. These skins were unpigmented, agreeing with the skins of first instar larvae described above. There had been no opportunity for the first instar larvae to have fed. Later however, 50×5 mm. millipeds were captured and eaten by the second instar larvae. As many as four larvae fed upon the milliped at the same time, all shared each large milliped.

A live Atopetholus michelbacheri (Verhoeff) milliped, approximately 25×2 mm. in size, was placed on the sand in a container and offered to first instar

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larvae. One larva captured it by the same method a mature larva would use. After disabling the milliped, the larva took it underground to feed. The next day, the milliped and the larva were shaken out of the sand and placed on top. Within a few hours, several first instar larvae were taking turns feeding on the milliped. At times, two larvae would feed side-by-side, their heads entering the milliped at the same time. Until this time, no one had successfully induced a first instar larva to feed.

This observation prompted an experiment to try and solve the feeding problem. The head of a large specimen of A. michelbacheri was severed with a scalpel and the milliped was placed on the sand in the Zarhipis container. Although they did not feed, in about 2 hours three Z. integripennis first instar larvae clustered around the milliped. The milliped's legs were still flexing. The next morning, one larva was feeding, by afternoon two were feeding side-by-side in the head of the milliped. Although a slight reflex action was still present in the last few pair of legs, the milliped was removed the next day to prevent possible spoilage and a new specimen of A. michelbacheri was decapitated and placed in the container. One larva began to feed within 5 minutes. The next day, seven first instar larvae were clustered around the milliped. All seven had fed as evidenced by the dark color in the intestines and by their turgid condition. Shortly after feeding on the milliped, the larvae withdrew underground. When they were shaken out 1 week later (to shake them out at this time was probably a mistake because they were found to be in a precast condition) and placed on clean moist sand, they remained on the surface curling and uncurling until one-by-one they died. As they died, they were preserved in alcohol. Upon examination, first instar larval skins were found to be loose over the second skin and in some cases the skin had split in a typical casting manner. It was also noted that three of the larvae had one clear eye at the base of each antenna and two black eye-like organs visible beneath the skin at the base of the head. With the exception of the two very black eyes at the base of the antenna, no other eyes were visible on the remaining larvae. The significance of this observation is probably involved with ecdysis.

Female Pupa

DESCRIPTION. The female pupa is larviform, capable of locomotion when disturbed, and brightly luminous. It has no pigmentation on the exoskeleton, or on the mouth parts. The lightly chitinized mandibles are translucent to trans-

Plate 3

LOWER FIGURE. Bicolored luminescence of the South American phengodid *Phrixothrix*. The larva is coiled with the anterior end in the center.

UPPER FIGURE. Luminous embryo larvae of Zarhipis integripennis still in egg.

PROC. CALIF. ACAD. SCI. 4TH SER., VOL. XXXV, NO. 12 (TIEMANN) PLATE 3







Specimen No.	Date collected	Date pupated	Date matured	No. days in pupal period
1	28 Dec. 1961	24 March 1962	5 April 1962	12
2	28 Jan. 1962	11 April 1962	24 April 1962 -	13
3	28 Jan. 1962	23 March 1962	4 April 1962	12
4	28 Jan. 1962	27 March 1962	8 April 1962	12
5	4 Feb. 1962	April 1962	13 April 1962	(Unknown)
		(Day unknown)		
6	11 Feb. 1962	26 March 1962	8 April 1962	13
7	Feb. 1962	15 April 1962	28 April 1962	13
	(Day unknown)			

TABLE 1. Pupal periods of laboratory reared female of Zarhipis integripennis.

parent, showing a small amount of orange-brown on the edges. Although rounded, the mandibles do not have a pore or mandibular setae. They are slightly tuberculate, meeting to only slightly overlap. This overlapping is not to the same degree as found on the larva and the adult. The antennae are transparent.

The developing adult eye organs are visible deep within the pupa. In some specimens these organs are located under the external pupal eye, in others, they are found posteriorly to the pupal eye. This gives a first impression that the pupa has four eyes.

The spiracles do not have a colored area next to them. They are of the same light white to buff color as the rest of the pupa. The strong setae present on the larva are reduced to soft, fine, white hairs on the pupa. The ring of setae encircling the anus on the larva is missing entirely from the pupa.

The tarsi have a light brown-orange tinge. Development was incomplete on one or two tarsi on all of the specimens examined. The deformity did not occur on the same tarsi on all specimens, but varied from specimen to specimen, nor did it carry over into the adult stage.

The concavities noted on the sternum of the larva and adult were not found on the pupa.

The female pupa, although it glows in the same manner as the larva, is much more brilliantly luminous. This brighter luminescence may be because of the transparency of the exoskeleton where light could pass through with little absorption. There are a total of 11 bright luminous bands located near the base of the meso- and metathorax and on all but the last abdominal tergum. A bright spot of light is also present on the upper half of the sides of the first nine abdominal segments, slightly below and behind the spiracles. One to three luminous spots, located on the sterna on the second through the ninth abdominal segments, sometimes connect to make a small circle.

MALE PUPA

DESCRIPTION. The male pupa is exarate with all appendages free and clearly transparent. The pupal genitalia are sometimes external and form a coil of one and one-half turns which tapers toward the end; in which case, the larval exuviae (on four of the pupae observed) remained attached to the end of the abdomen and formed a loose cocoon that covered the genitalia. When the pupal genitalia were internal, the larval skin was free of the pupa on two other pupae observed in this study.

The mandibles are the first structures to become visible in the pupal skin. Externally, the legs and antenna appear as transparent cylindrical sacs with slight constrictions indicating the joints. The orange color begins to appear on the head, thorax, abdomen, and legs approximately 5 days before the adult emerges from the pupa. Two days before emergence, the black antennae and rami are clearly visible. The black color of the eyes, the tarsi, and the tarsal claws may also be seen. The dark wings and elytra and the fine hairs on the elytra are also visible.

The pupal skin is shriveled against the insect prior to the emergence of the adult. The pupa writhes and turns periodically until the pupal skin splits and the adult is able to emerge. Newly emerged males of Z. *integripennis* differ from males collected in the field in that the elytra take several hours (overnight) to become fully pigmented, the abdomen is swollen, a white fatty structure is visible inside the transparent pleura, and in the teneral stage, the male is still luminous. During the post-pupal stage that is apparently experienced by the adult male, the abdomen becomes progressively thinner and luminescence gradually disappears, or is hidden by the orange color of the abdominal tergal and sternal plates. The insect is ready to fly at about the same time as the luminescence disappears. This may explain reports of luminescence of male Z. *integripennis* made by some authors—reportedly, the phenomena has been observed only on the night the insect was captured and not subsequently.

OBSERVATIONS. Of the six male pupae observed in this study, one was collected by Mr. L. W. Nichols from Short Canyon in 1960. Five were collected by the author in 1962 and 1963 from the alluvial fan at the mouth of Short Canyon. The pupal period of the males ranged from 20 to 35 days.

Males reared in a laboratory have lived as long as 9 days. Field collected specimens usually live from 3 to 4 days, although some have survived for as long as 1 week. Survival of the males is enhanced by keeping them in a high-humidity environment such as a closed container with a fresh sprig of live plant.

One male larva was observed 1 hour before ecdysis. At this time, the mandibular setae were displaced out of the channel, the thorax was swollen, but the abdomen, although possibly a little thinner, appeared normal. When viewed

from beneath, the larval body fluid could be seen moving rapidly about inside the abdomen. There were many small beads of clear fluid on this specimen. When next observed (about 1 hour later), the larval exuviae had split from the head to the abdomen along the medial line on the dorsal surface. The pupa had half emerged from the larval exuviae and was glowing brightly. The eves were a slight pink in color with a black area deep inside. The rest of the pupa was very white and transparent. At first glance it appeared to glow all over, but when viewed under a microscope it was apparent that the glow came from very definite areas. All of the specimens of Z. tiemanni Linsdale collected in the field glowed when viewed after 1 to 3 minutes of eve accommodation. Twothirds of the field collected Z. truncaticeps Fall specimens examined under these conditions were luminous. The apparent conclusion is that luminosity has no survival value to the adult male. However, males of the *Phrixothrix* observed by the author in November, 1960 at Sâo José dos Campos, Brazil, became brightly luminous when captured or disturbed although they are not normally luminous. A larger species of *Phrixothrix* observed in January, 1963 at the same locality behaved in the same manner.

Adult Female

DESCRIPTION. The adult female of Z. integripennis is larviform throughout life (the adult male is winged), differing little in external appearance from the larva. When teneral the adult female varies in color from white to buff, acquiring dark gray triangular markings on each side of the terga of the abdomen and thorax in about 12 hours. The colored area anterior to the spiracles on one specimen from Short Canyon returned to a dark brown and the tergal coloring remained triangular throughout life. The triangular colored areas on a specimen from the Berkeley area filled in after about 3 days, making a single dark rectangle that was bordered with a buff area across the terga and crossed by a medial suture.

The larval setae are missing from the sterna, the tenth abdominal segment, and the tergum of the ninth abdominal segment on the adult female. The setae on the tergum of the prothorax are the same as found on the larva, however.

The female oppore is hidden by a large fold on the underside of the ninth abdominal segment. The fold reaches from one side of the sterna to the other in a long arc bordering a deep pouch with the oppore at the bottom center of the pouch.

The eyes of the adult female are black, the mandibles are shaped once again as in the larva (thin, heavily chitinized, and overlapping but more rounded).

Although several adult females were offered live millipeds (*Atopetholus*) during this study, none were observed to have been killed or eaten.

MATING

There have been no reports of observations made of Z. integripennis mating under completely natural conditions. However, experimental data suggests that males are attracted to females by scent. The distance from which a female is capable of attracting a male is not known. Also evident is the fact that more than one male will mate with a single female.

The males, although ordinarily peaceful insects, will use their sharp curved mandibles to fight each other when in the presence of a female. Such fights usually result in fatal injury to one of the males.

Once a male reaches a female he appears to be guided by proprioceptive cues. He will mount the female at the anterior nearly as often as he will mount the posterior. In some instances, a female will curve in an attempt to move the male to the proper position. In other instances, after several unsucessful attempts at mating at the anterior, the male will momentarily leave the female. Upon his return he will again attempt to mate, continuing in this manner until properly positioned on the female (facing forward with the abdomen curved under the female from the side) and coitus takes place.

Essentially, the male genitalia consists of (1) a pair of claspers, (2) a chitinized tube with a closed rounded end and an opening positioned half way down from the tip, and (3) a long thread-like aedeagus. The female is pinched with the claspers and the tube is forced into the sternum of the ninth segment anterior to the oopore. The aedeagus emerges from the tube through the opening and into the female for the transfer of the sperm. The tube and the aedeagus may be observed on pinned specimens. The same mechanism has been found on *Phrixothrix* when nondestructive examinations of collections have been made. Illustrations of the male genitalia of *Phrixothrix* may be found in Costa Lima (1953).

OBSERVATION. In the course of this 6-year study, a great many experiments were performed, providing a greater knowledge of the mating habits of Z. *integripennis*.

An experiment made by D. D. Linsdale, wherein he observed that males were attracted to an empty container in which a female had recently been removed, was repeated with desert specimens. An adult female was carried to the mouth of Short Canyon and transferred to another container. The two containers were placed about 40 feet apart. Within 15 minutes seven males approached the female and two males went to the empty container. The males were first observed approximately 2 meters from the containers walking in a relatively straight line. At no time in this case, or in any of the other experiments, were males observed to fly to the females. During another experiment, female Z. integripennis were carried in plastic refrigerator jars to an area about 4 miles northeast of Inyokern, Kern County, where two species of Zarhipis are

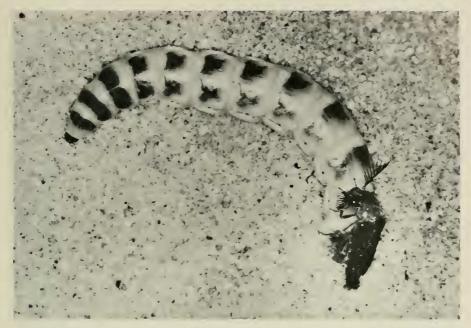


FIGURE 9. Mating of Z. integripennis.

sympatric. Both Z. integripennis and Z. tiemanni males were attracted to the females.

Both Linsdale (1961) and Williams (unpublished notes) observed that males will approach females during the day in the humid coastal areas. Although males were not observed to approach females during the day in the low relative humidities of the desert environment, they did come to the females at dusk. One such observation was made 18 April 1962. These males were attracted to the females within 10 minutes after sunset when the air temperature was 25° C. They continued to arrive for about 35 minutes. During this time, the temperature had dropped to 18° C. and the glow from the females was barely visible in the twilight. The experiment was stopped at this point because of increasing winds.

Four virgin females of Z. integripennis were exposed at the mouth of Short Canyon on 13 April 1962. At the time they were exposed (9:00 P.M.), the temperature was 21°C, with winds estimated at 5 miles per hour or less. Within 5 minutes, six males appeared. When no other males approached after another 10 minutes, the females were moved one-fourth mile north. Here, five males approached within 15 minutes. Data from this experiment suggests a density for males, but many other influences may have been involved. All of

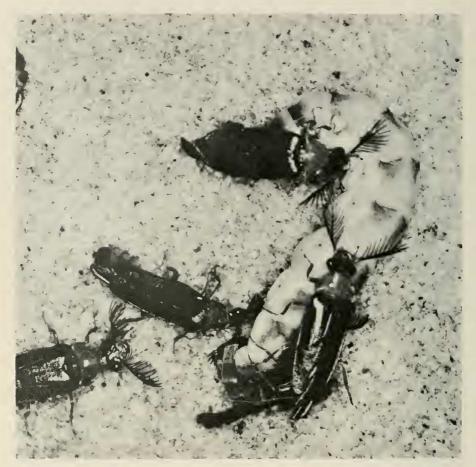


FIGURE 10. Attracted by scent, a number of males of Z. integripennis will come to a single female.

the males observed in this experiment were examined for luminscence after 5 minutes of eye accommodation. No luminescence was apparent.

A normal mating of Z. integripennis with Z. integripennis, collected from the same locality, was allowed to take place. Four males were placed in a container with one female. Two males successfully mated with the female. Two of the males approached the female, one mating with her almost immediately. The other two immediately attacked each other using their mandibles as weapons. The fight continued for quite some time, with the males twisting and turning to make the most effective use of their mandibles, sometimes grabbing each other, and sometimes lifting each other in the air. Finally, one of them completely disabled the other by puncturing its thorax.

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FIGURE 11. Close-up of Z. integriptennis mating. The insects were frozen with liquid nitrogen for photography. The chitinized portion of the genitalia have come out of the female, but the sperm transfer organ is still in the ninth abdominal segment.

In a cross-mating experiment, seven males of Z. tiemanni were placed in a container with one female of Z. integripennis. The behavior was much the same as in the normal mating with a considerable amount of fighting among the males. That mating had actually occurred was verified by gently pulling the female from the male during coitus to see if he was pulled along by the aedeagus. This female produced no eggs, nor did she go into the ovulating stage, although she lived for over a month and was mated with males of Z. tiemanni on two occasions.

If females were not allowed to mate soon enough, they failed to mate at all when offered males. A 28-day, mature, virgin female prevented a male from mating by curling up; however, she did exhibit some of the changes that take

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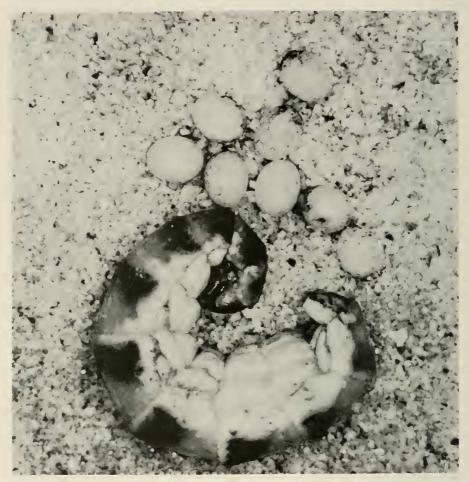


FIGURE 12. Female of Z. integripennis with eggs. The thin thorax is characteristic of the ovulating stage.

place with egg laying—a thinning of the thorax and a swelling of the abdomen, and produced nine eggs. The eggs—the largest was twice as large as the smallest—finally molded, shriveled, and turned black.

PLATE 4

UPPER FIGURE. Males of the three known species of Zarhipis-Z. integripennis, Z. truncaticeps, and Z. tiemanni.

LOWER FIGURE. Underside of males of Zarhipis integripennis, Z. truncaticeps, and Z. tiemanni. PROC. CALIF. ACAD. SCI. 4TH SER., VOL. XXXV, NO. 12 (TIEMANN) PLATE 4







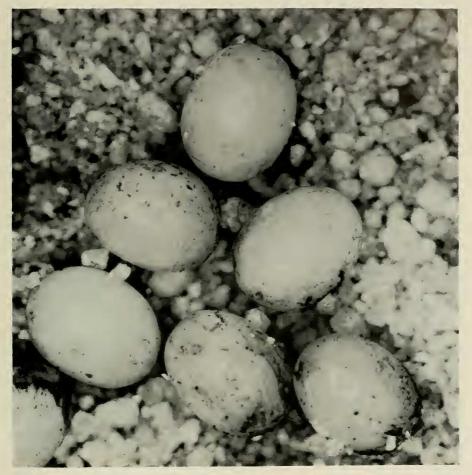


FIGURE 13. Freshly laid eggs of Z. integripennis.

FEEDING BEHAVIOR

Larval phengodids, not restricted to a species-to-species relationship, feed on various species of millipeds. *Zarhipis* in captivity have been observed to capture and feed on most of the milliped species offered, even when the millipeds belonged to different orders. No evidence has been uncovered to prove that adult phengodids feed.

The method used by *Zarhipis* to capture and feed indicates a long and close association with millipeds and is so specialized that it is reasonable to presume that all phengodids prey on millipeds.

DESCRIPTION. When a *Zarhipis* larva discovers a milliped, it races alongside the milliped until it can mount its back. (The walking legs of the larva are used



FIGURE 14. Female of Z. integripennis in act of egg laying.

only in the chase. They are not used to disable the milliped.) When mounted, the larva throws a coil around the milliped with its last abdominal segments and uses the tenth abdominal segment in an opposable manner to aid its grip. It then stretches full length to reach for the most vulnerable part of the milliped's exoskeleton—the articulating membrane (where the main nerve is near the surface) between the head and the first body segment on the ventral side. The larva severs the main nerve with its sickle-shaped mandibles, paralyzing the milliped. When this has been accomplished, the larva turns its body so that its head is upside down and its legs are facing away from the milliped as it bites. If a capture takes place above ground, the *Zarhipis* larva leaves the milliped after it is paralyzed, and goes underground. Here the larva turns around to emerge head first, takes the milliped's antenna in its mandibles and tows it underground.